Plant Ecol (2012) 213:259–272
DOI 10.1007/s11258-011-9972-5

Landscape responses to a century of land use along the northern Patagonian forest-steppe transition

Juan H. Gowda · T. Kitzberger · A. C. Premoli

Received: 12 April 2011 / Accepted: 8 September 2011 / Published online: 30 September 2011

Abstract Land use history reconstructions in temperate regions of the Northern Hemisphere indicate that periods of deforestation are often followed by natural afforestation, so that the long-term outcome at the landscape level will be a balance of retractions and advances of plant communities associated with varying local land uses. During the last decades of the XIX century, large forest areas were cleared in Northwestern Patagonia to open farmland. In this article, we compared historical land use/land cover maps with land cover maps derived from Landsat images to analyze the factors that may have influenced the dynamics of land cover change of the forest-steppe ecotone during the last 100 years. Our results indicate that Patagonian forests underwent a rapid initial recovery after the extensive fires of last century, replacing mainly shrublands. More than 50% of the old burns are currently covered by forests, and modern fires affect areas characterized by fire-prone vegetation. Whereas natural afforestation is an ongoing process positively associated with moisture, the rate of forest losses has increased during the last three decades, concentrating on xeric aspects and the vicinity of roads. We conclude that the outcome of the dynamics between fire-intolerant forests and fire-prone plant communities will largely depend on human-related activities, modeled by structural features of the landscape (i.e., topography, dominant winds), and processes triggered by past land uses.

Keywords Forest expansion · Anthropogenic impacts · South America · Fire · Tree plantations

Introduction

Recognition of the influence of current and past human activity on the structure and functioning of ecosystems has led to an appreciation of regional/historical perspectives as tools for anticipating future scenarios (Foster et al. 2003; Schulte et al. 2007). Many temperate and tropical regions of the globe have witnessed a recent sequence of intensification in land use related to a period of settlement mostly associated with logging, large fires, and expansion of agricultural land, followed by post-settlement decline or abandonment of farming activities (Grau et al. 2003; Rhemtulla et al. 2007). Because abandonment of farmland has often triggered processes of natural afforestation (Graham et al. 1963; Petit and Lambin 2002; Hall et al. 2002), the long-term dynamics of plant communities at the landscape level will be associated with the spatial and temporal distribution of local land uses and

J. H. Gowda (✉) · T. Kitzberger · A. C. Premoli
Laboratorio Ecotono, Universidad Nacional del Comahue, INIBIOMA-CONICET, Quintral 1250, 8400 Bariloche, Argentina
e-mail: juan.gowda@gmail.com

the capacity of the different plant communities to respond to these uses (Grau et al. 2008).

For northern Patagonia, it has been generally assumed that the demise of the aboriginal culture that used fire for hunting larger herbivores, as well as the post-settlement reduction of Euro-Argentinean farmers, combined with a long-term regional reduction in herbivore numbers (Veblen and Lorenz 1987, 1988; Kitzberger and Veblen 1999) may have triggered an expansion of forests on shrublands and grasslands. In contrast to this pattern, recent studies indicate that during the last three decades a rebound in fire activity has taken place, affecting large areas of mature *Nothofagus* and *Austrocedrus* forests (Bruno and Martín 1982; Mermoz 2002).

Fire regime reconstructions based on fire scars and stand initiation smaps indicate that fire frequency peaked 1860–1880 along the transition zone between dry *Austrocedrus chilensis*/*Araucaria araucana* woodland and steppe as a result of intense fire use for hunting, and showed a systematic reduction along the whole region following the demise of aboriginal cultures (Kitzberger and Veblen 1997). In contrast, fire frequency in the more mesic *Nothofagus* peaked between 1890 and 1920 as a result of systematic use of fires for opening farmland, being very low since then (Kitzberger et al. 1997; Veblen et al. 1992a, 1999). More recently, drought-driven large, severe fires often initiated in shrublands close to roads and urban areas, have recently turned into large areas of forests to shrublands (Mermoz et al. 2005).

Cattle and sheep breeding became the main economic activities of Euro-Argentinean settlers in forest and grassland areas, respectively. Livestock numbers peaked during the mid 20th century and are declining since then (Eriksen 1971). The direct impact of grazing by livestock and introduced herbivores on tree regeneration has been extensively documented in the region (Veblen et al. 1992b; Kitzberger et al. 2005; Raffaele et al. 2011).

Since 1970, pine plantations have been promoted as an alternative land use for abandoned farmland in Patagonia, leading to the introduction of several fire-adapted species such as *Pinus ponderosa*, *P. contorta* var. *latifolia*, and *P. radiata* (Schlichter and Laclau 1998). Also, drought-induced adult tree mortality is becoming a major factor for landscape level shifts toward drought tolerant trees and/or shrubs (Suarez and Kitzberger 2008, 2010), further increasing the flammability of forests. The pattern of distribution of this new land use may both affect the successional path from shrubland to native forest, and the flammability of the land cover through time.

During the last decades, considerable population growth (8.4–21.3% increase 1991–2001) and rapid urbanization (79.9–84.4% urban population from 1991 to 2001) has occurred in Northern Patagonia (INDEC 2001). Because most modern fires are associated to roads and shrublands (Mermoz et al. 2005), the rapid population increase of the population in the region may lead to increasing rates of fire ignition.

Combining century-old historical land cover maps with a three decade-long remote sensing dataset, we analyzed whether historical legacies (past fires, remnant forest, and fire-prone communities), current disturbance regimes (human-set fires), and expanding land uses (urbanization, roads, exotic pine plantations) have affected land cover dynamics during the last century over a broad region (550,000 ha) of Northern Patagonia. We addressed the following questions: (1) are Patagonian forests recovering from the period of extensive fires associated to settlements? (2) if so, which vegetation covers are being replaced by forests? (3) has the area affected by fires been reduced during the last 100 years? (4) which vegetation types have colonized old fires? (5) which land cover types are being affected by modern fires? (6) can we associate simple environmental and human-related variables with the processes of afforestation and deforestation?, and (7) did the relative and absolute importance of these processes change during the last 100 years?

Methods

Study area

The study area is a rectangle located at the forest-steppe ecotone in northwestern Patagonia Argentina (Fig. 1) within the following corner coordinates: NW: 38°44′S, 71°25′W; NE: 38°46′S, 70°48′W; SW: 43°05′S, 71°35′W; SE: 43°05′S, 70°55′W. Total study area after masking non-classified pixels of all images, high altitude plant communities, lakes and non-surveyed areas of the historical map was 540,360 ha.

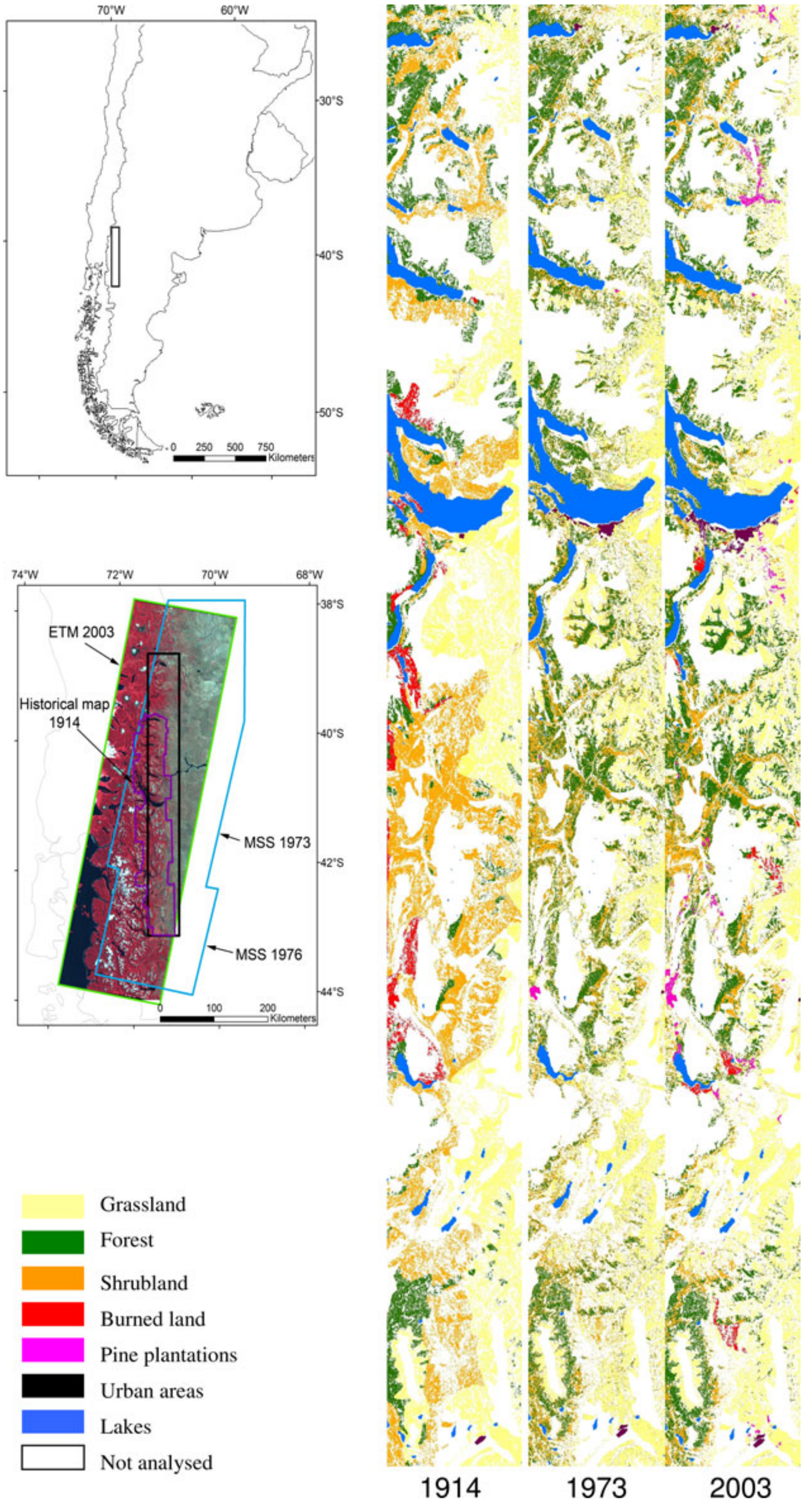


Fig. 1 Land cover maps along the transition zone between forests and grasslands of Northern Patagonia during the last century. Areas above 1500 m.a.s.l. as well as those classified as agricultural land in 1914 and non-classified pixels are shown as a *white* mask

Remote sensing data

The study area covered portions of four LANDSAT scenes for each date (source: MSS 3/21/1973, TM—3/7/1985, TM—8/3/1997, and ETM—2/13/2003 Path 248, rows 87–90 for all mosaics). Imagery was selected for low cloudiness and similar phenological state. All images used had <5% clouds (outside study area) and were taken between mid summer-early fall. TM images were radiometrically and geometrically standard-terrain corrected (L1T). All images were resampled using UTM Datum and WGS84, 19S projection. Atmospheric corrections were performed using ATMOSC (Idrisi Andes 2006).

Land use/land cover (LULC) classifications

We performed a supervised maximum likelihood classification (MAXLIKE; Idrisi Andes 2006) on the image mosaics for years 1973 and 2003 using 432 and 520 training plots, respectively, with higher sampling intensity for forests, intermediate intensity for grasslands, shrublands, and plantations, and low-intensity for urban areas, water, and absolute shade (Table 1). All training plots were taken in areas known to have remained stable during the period 1973–2003, so that a common set of training plots could be used for the classification of all dates. Approximately 10% of the plots were allowed to remain unclassified to avoid forcing uncertain pixels into specific classes.

Assessment of areas burned 1973–2003

Burned areas were estimated through decadal differences in normalized difference vegetation indices (NDVI) and superimposed to the final classification. Because of unavailability of pre-1973 images, burned areas in 1973 were derived from $NDVI_{03}$–$NDVI_{73}$, i.e., assuming that 1973 burns had recovered in NDVI by 2003. Burned areas in 1985 were determined from $NDVI_{73}$–$NDVI_{85}$, areas burned 1997 were determined from $NDVI_{85}$–$NDVI_{97}$, while those in 2003 were derived from $NDVI_{85}$–$NDVI_{03}$. This technique has proven to be useful in detecting large fires (Mermoz 2002).

Classification accuracy

Accuracy of the image classification was assessed using a confusion matrix (omission error and commission error for every class) based on 520 control points (198 points for forests, 143 for shrublands and wet grasslands, 132 dry and high-elevation grasslands, 34 exotic pine plantations, and 13 points for urban

Table 1 Confusion matrices for supervised classification of two landsat mosaics

	Forest	Shrubland	Grassland	Plantation	Urban
1973					
Forest	108	30	1	0	0
Shrubland	43	96	1	0	0
Grassland	10	3	120	0	4
Plantation	0	0	0	7	0
Urban	0	0	0	0	9
Total	161	129	122	7	13
Omission errors	0.329	0.256	0.016	–	0.31
Commission errors	0.19	0.34	0.14	0.00	0.00
2003					
Forest	166	14	0	0	0
Shrubland	19	124	0	0	0
Grassland	12	4	132	0	1
Plantation	0	1	0	34	0
Urban	1	0	0	0	12
Total	198	143	132	34	13
Omission errors	0.16	0.13	0.00	0.00	0.08
Commission errors	0.07	0.13	0.13	0.03	0.08

areas). Agreement between ground control points and mapped classes varied between 0.69 (1973) and 0.86 (2003).

Highest omission and commission errors corresponded to forests and shrubland classes (Table 1). The Maximum Likelihood classification produced rather symmetric errors between shrublands and forests, i.e., a portion of forest were misclassified as shrublands and a similar portion of shrublands was misclassified as forests. Urban areas, dry grasslands, and plantations had low classification error levels (Table 1).

To estimate the accuracy of the method for detecting modern fires, all areas classified as fires larger than 1,000 ha were individually checked with fires reported by the National Fire Management Plan (PNMF) during the same period. 81% of the burned areas detected using differences in NDVI corresponded to large fires documented by the PNMF, comprising 84% of the area reported as burned during the period 1970–2003. The method used here is likely to underestimate grassland fires because of the rapid recovery of the vegetation cover of this plant community.

Historical map

Color copies of the vegetation and land cover maps produced by Willis (1914) covering of the whole study area were scanned and georreferenced using the Landsat image mosaics (see above), a digital elevation model (DEM) with 30 m resolution (http://asterweb.jpl.nasa.gov/gdem.asp), river, lakes, and road maps as background. LULC classes were manually digitalized using the following methodology.

Forests were digitalized maintaining shape and size of original patches and repositioned at the most likely location based on topographic attributes (i.e., aspect slope and altitude, rivers, lake shores, and peaks).

Burned land had often clear boundaries such as rivers, lakes, and elevation lines. The upper limit of burned land was given by altitude lines when existing, or by the mask of 1500 m a.s.l.

Shrublands and grasslands Rivers and mountains, which in most cases delimited the two cover types, were used to improve the accuracy of the boundaries between them. In the absence of such physical attributes the original division line of the historical map was used.

The following cover classes originally mapped by Bailey Willis were excluded (masked) from the analyses:

Mountain forests and grasslands cited as above 1500 m a.s.l. were excluded from the analysis because the original land class did not discriminate between forests, grasslands, high altitude vegetation, and rocky outcrops. This class has very low accessibility for humans and was probably marginally affected by old fires. Likewise, all areas above this altitude are currently not affected by urbanization or forest plantations, even though they may be marginally affected by large fires.

Agricultural land was masked because the original map did not make differences between grasslands, recently burned shrublands, and cultivated areas, not allowing any comparison between these categories.

Lakes Because the lakes of the study area did not show any significant change during the last 30 years, they were assumed to have remained unchanged during the last 100 years. Lake shores, islands, and rivers from the original map were used to anchor the main vegetation classes of the original map to those derived from image interpretations.

LULC change analysis

The classified images and original historical were converted to raster maps in Idrisi Andes to calculate total area covered by each class, gains, losses, and transitions between classes. Transitions between all land cover/land use types were calculated using CROSSTAB (Idrisi Andes 2006) for the whole period (1914 vs. 2003) as well as for two sub-periods (1914 vs. 1973 and 1973 vs. 2003). Net expansion/retraction was calculated by subtracting the transition values for the different classes. Gains were calculated as the transition from all classes to any specific class, whereas losses are the transitions from the focal class to other classes. Net contribution to forest expansion was calculated using a cross tabulation matrix (CROSSTAB, Idrisi Andes 2006) between the forest area at the end of any given period and the complete land unit map at the beginning of the study period. The relation between aspect and gains and losses of forest and scrubland was calculated using a cross tabulation matrix (see above) between a raster of the differences in distribution of the above named vegetation types and a classified raster of the aspect data derived from the DEM of the study area (see below).

Analyses of forest gains and losses

As predictors of the changes in LULC, we used aspect (i.e., the slope facing direction) divided in Northing and Easting (i.e., cosine and sine-transformed azimuth values, respectively), slope (i.e., steepness), and altitude derived from the SRTM90 DEM. Because the whole study area is located in the southern hemisphere (>38° South), northern aspects receive significantly higher radiation than southern aspects, in particular when associated with steep slopes, leading to more xeric conditions. Western aspects are most exposed to the dominant westerly winds of the region, being associated at the local level with higher precipitation and a lower frequency of frosts. Mean annual precipitation was taken from the Woldclim dataset (Hijmans et al. 2005). Raster maps of distance to roads, water, grasslands, and shrublands were generated using DISTANCE (Idrisi Andes 2006). The road layer in the National Grid (SIG IGN 250, http://sig.ign.gob.ar/home.asp) was used for this analysis.

To estimate the importance of the above named variables in influencing forest gains and losses, we used logistic regression analysis. Binary response variables were new forests and lost forests for the total period 1914–2003 and for the sub-periods 1914–1973 and 1973–2003.

To reduce autocorrelation, we sampled the raster layers corresponding to the response and predictor variables within a 1 × 1 km systematic sampling grid. For the analysis of forest gain, all forests at the beginning of the analyzed period were masked to avoid redundant zeros. Similarly, for the analysis of forest losses, only the areas with forest at the beginning of the period analyzed were sampled and the rest of the study area was masked. To avoid an unbalanced dataset (i.e., a high proportion of zeros in forest gain analysis and a low proportion in the forest loss analysis) the subset of data was randomly re-sampled until the difference between 0 and 1 was within 5%. The effect of each predictor variable on the occurrence of forest gain or forest loss was evaluated by multivariate logistic models. Initial variable selection was conducted through a backward stepwise model allowing variables with $P > 0.005$ to be retained. The final model was selected using the best subset of variables on the basis of the Akaike IC procedure.

Results

Patterns of change in land cover

Forests are the most expanding cover type of the region for the whole period (Figs. 1, 2), covering today more than 25% of the study area (Table 2), i.e., 65% more than in the early 20th century which represents a net increase of forest cover of 9.7% over the entire study region. This expansion took place mainly at shrublands and burned areas, replacing 50 and 61% of these land cover classes, respectively (Table 3; Fig. 3). Forest expansion occurred chiefly during the first period (1914–1973) at a rate of 978 ha of new forests per year (0.18% per year increment over the study area), showing a marginal decline during the period 1973–2003 (Table 2). Only 36% of the forests detected by 2003 were classified as such in 1914 (i.e., potentially remnant forests) indicating that most existing forests established during the last 100 years on non-forest cover types of the early 20th century. The trend of forest replacing shrubland was maintained between 1914–1973 and 1973–2003 but was an order of magnitude lower during the later period (Fig. 3). Burned areas and grasslands showed also a positive contribution to forest expansion during the period 1914–1973, but this pattern reverted since then (Fig. 3). Urban land and plantations had a marginal negative net contribution to forest cover throughout the period (Fig. 3).

Shrublands showed a continuous retraction during the study period (Fig. 2), covering today less than 17.1% of the study region (Table 2); a reduction of 46% from the area covered at the beginning of the period. Even though the total retraction of shrublands was highest during the period 1914–1973, the annual rate of retraction was highest during the period 1973–2003 (Table 2), indicating that the transition from shrublands to other land cover types is an ongoing process.

Forest plantations increased 15-fold during the last 30 years of analysis showing an expansion of 92 ha $year^{-1}$ (Table 2), but had a minor contribution to the land cover changes of the study area (0.02% $year^{-1}$, Fig. 1). Most forest plantations were established on former shrublands (49%) and grasslands (29%). In addition, 20% of the plantations mapped in 2003 were established on land covered by forests in 1914 (Fig. 2). Urban centers expanded almost

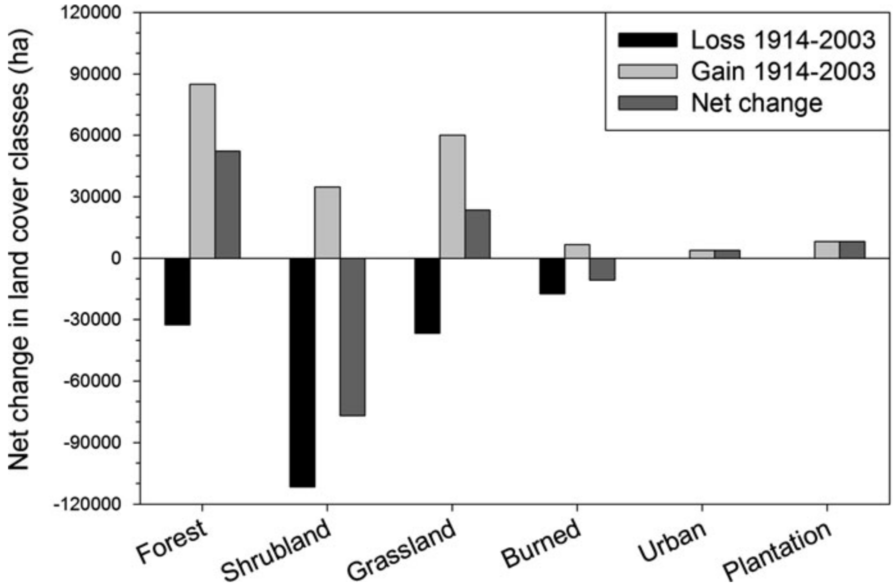


Fig. 2 Gains, losses and net change in the area of main land cover classes along the transition zone between forests and grasslands of Northern Patagonia during the period 1914–2003

Table 2 Landscape composition and rates of change of land cover classes within the study area

Period	Forest		Shrubland		Grasslands		Plantations		Urban		Recent fires	
Main vegetation cover classes (hectares & percentage of study area)												
1914	80,601	15%	169,621	31%	272,146	50%		0%	427	0%	17,565	3.3%
1973	138,294	26%	121,084	22%	278,012	51%	651	0%	2,304	0.4%	16	0%
2003	132,827	25%	92,639	17%	295,687	55%	8,226	1.5%	4,176	0.8%	6,804	1.3%
Annual rate of change (hectares and percentage of change per year)												
1914–1973	977.84	1.2%	−822.66	−0.5%	99	0.0%	11		32	7%	−297	−1.7%
1973–2003	−182.22	−0.1	−948.15	−0.9%	589	0.2%	253	9.4%	62	2.1%	226	8.5%
1914–2003	586.81	0.7	−864.96	−0.5%	264	0.1%	92		42	9.9%	−121	−0.7%

Recent fires are presented as an independent class because they may trigger transitions between the main vegetation classes

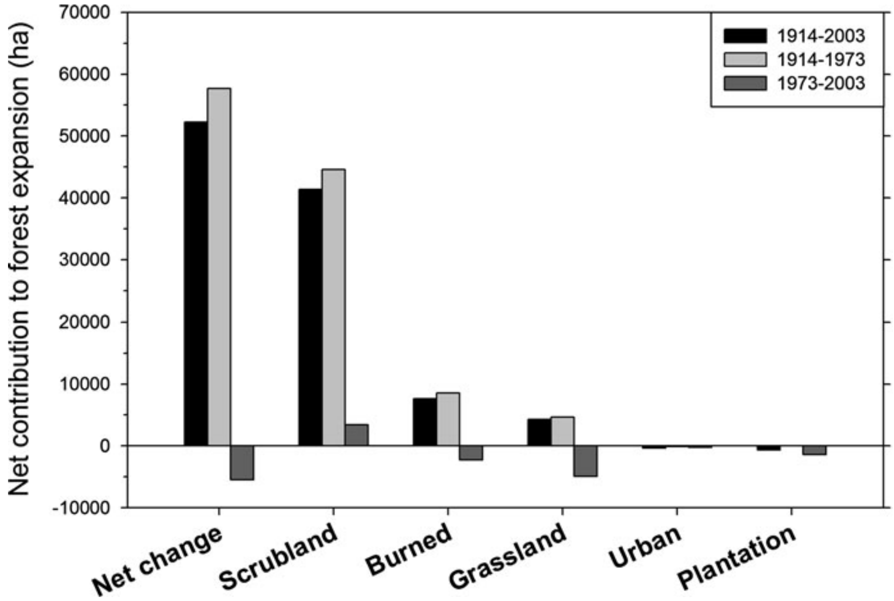
Table 3 Short and long-term relation between fire and land cover

	Forest	Shrubland	Dryland	Plantations	Urban	Recent fires	Total
Burned area 1914	Current (year 2003) land cover class of land burned 1914						
Hectares	8,838	5,163	2,106	1,187	91	180	17,565
% of burned area	50%	29%	12%	7%	0.5%	1.0%	100%
% of current cover	7%	6%	1%	14%	2%	4%	3.3%
Burned area 1973–2003	Historical (year 1914) land cover classes affected by fires 1973–2003						
Hectares	2,305	6,733	1,411	–	–	1,275	11,723
% of burned area	20%	57%	12%	–	–	11%	100%
% Burned/% available	1.32	1.83	0.24[l]	–	–	3.35	1.00

a Most fires mapped 1914 are today either forest or shrubland, b fires and schrubland mapped 1914 were more affected by recent fires than any other land cover class

tenfold since 1914 (42 ha year^{-1}), replacing mainly grasslands and shrublands (48 and 31% of former grasslands and shrublands, respectively) account in 2003 for 0.8% of the study area (Table 2). Grasslands are a relatively stable cover type (87% of their area without changes, Table 2), showing a marginal

Fig. 3 Contribution of main land cover classes to changes in forest cover along the transition zone between forests and grasslands in Northern Patagonia during the periods 1914–1973 and 1973–2003



but steady expansion during the entire period of 0.1% $year^{-1}$.

Patterns of change in area burned

Newly burned land covered a total of 17,565 ha 1914 (i.e., 3.3% of the study area, Table 2), decreased in 1973 to only 16 ha (Table 2) increasing again in 1985 and 1997 (2,269 and 2,671 recently burned, respectively) and showed a new increment in 2003 (6,804 ha, Table 2). The sum of areas detected as burned in the four mosaics (1973, 1985, 1997, and 2003) is equivalent to 67% of the area burned 1914, indicating a very important reduction in vegetation affected by fires during the last 30 years.

Areas burned in 1914 are today mostly covered by forests and shrublands (50 and 29%, respectively) comprising 6 and 7% of the current area of these land cover classes, respectively (Table 3). 14% of the forest plantations were established on areas affected by old fires (Table 3). 12% of the area burned 1914 is today covered with grasslands, accounting for less than 1% of the area covered by this land cover class (Table 2).

Analysis of the distribution of recent fires (1973–2003) indicates that old fires and shrublands were more affected than other land cover classes (Table 3). 7.3% of the area mapped as burned 1914 was affected by fires during this period, three times more than expected by the proportion of burned land in the study area (Table 3). At the same time, shrublands accounted for 57% of the area burned, whereas forests were slightly more burned than expected. Grasslands were marginally affected by recent fires, accounting for 12% of the burned area (Table 3).

Main variables influencing landscape change

Forest expansion

For the entire period of analysis (1914–2003), forest expansion was associated with southern aspects, closeness to preexisting forests, and the replacement of shrublands (Table 4). All variables had a better explanatory power for the period 1973–2003 (Table 4). During the period 1914–1973, the most important variable explaining forest gain is replacement of shrublands, followed by distance to forest and southern aspects (Table 4). For the latter period (1973–2003) distance to forest becomes the main explanatory variable, followed by aspect and replacement of shrublands (Table 4). Average distance between new and remnant forests shifted from 3,100 m for the period 1914–1973 to 60 m for the period 1973–2003, indicating a lower resolution of the land cover map of 1914 than the maps derived from LANDSAT image interpretations. Precipitation, western aspects, and distance to roads were significant variables during the first period whereas elevation became a statistically significant variable during the last 30 years (Table 4).

Table 4 Main drivers of forest expansion for the entire period (top 1914–2003) and two sub-periods (mid 1914–1973 and bottom 1973–2003)

	Estimate	Sd error	Wald stat	*P*
Forest growth 1914–2003				
Intercept	1.083938	0.259902	17.3936	0.000030
Distance to forest	−0.000115	0.000018	42.0315	0.000000
Precipitation	0.001459	0.000280	27.0570	0.000000
North	−0.621880	0.087953	49.9930	0.000000
Distance to road	0.000140	0.000020	47.3392	0.000000
Former shrubland	0.769125	0.060284	162.7751	0.000000
AIC	1831			
L. Radio χ^2	503.4	Odds ratio:	6.96	
P	0.000000	Log odds	1.94	
Classification	Pred. 0	Pred 1	% correct	
Observed 0	592	247	70.6	
Observed 1	214	622	74.4	
Forest growth 1914–1973				
Distance to forest	−0.000127	0.000014	79.8104	0.000000
Precipitation	0.000494	0.000112	19.2988	0.000011
East	−0.376738	0.081283	21.4820	0.000004
North	−0.548795	0.084741	41.9402	0.000000
Distance to road	0.000051	0.000019	7.4886	0.006209
Former shrubland	0.847700	0.057978	213.7722	0.000000
AIC	1953			
L. Radio Chi sq	447.3	Odds ratio:	7.63	
P	0.000000	Log odds	2.03	
Classification	Pred. 0	Pred 1	% correct	
Observed 0	622	266	70	
Observed 1	208	679	77	
Forest growth 1973–2003				
North	−0.575709	0.161604	12.69112	0.000367
Elevation	0.001184	0.000135	76.45576	0.000000
Distance to forest	−0.010368	0.001156	80.39884	0.000000
Former shrubland	0.931846	0.111432	69.93085	0.000000
AIC	602			
L. Radio Chi sq	607.6	Odds ratio:	37.45	
P	0.000000	Log odds	3.62	
Classification	Pred. 0	Pred 1	% correct	
Observed 0	363	87	81	
Observed 1	43	386	90	

Variables were selected by step-wise regression followed by AIC test of the best models

Forest losses

For the whole period (1914–2003), the main variables consistently associated to forest retraction were precipitation (dry areas), closeness to water (areas nearby rivers and lakes), as well as aspect and elevation (north slopes and low-elevation sites; Table 5). Between 1914 and 1973, forest losses were

Table 5 Main drivers of forest losses for the entire period (top 1914–2003) and two sub-periods (1914–1973 and 1973–2003)

	Estimate	Sd error	Wald stat	*P*
Forest loss 1914–2003				
Intercept	7.20760	0.855423	70.99357	0.000000
North	0.57119	0.124309	21.11323	0.000004
Elevation	−0.00183	0.000364	25.20667	0.000001
Precipitation	−0.00526	0.000671	61.50470	0.000000
Distance to water	−0.00049	0.000105	21.40731	0.000004
AIC	1124		Odds ratio:	4.43
L. Radio Chi sq	121.1		Log odds	1.49
P	0.000000			
	Pred. 0	Pred 1	% correct	
Observed 0	278	89	76	
Observed 1	134	190	59	
Forest loss 1914–1973				
Intercept	3.10979	0.512446	36.82700	0.000000
Precipitation	−0.00264	0.000572	21.28808	0.000004
Distance to grassland	−0.00004	0.000013	9.23759	0.002371
Distance to water	−0.00047	0.000097	23.82080	0.000001
AIC	898			
L. Radio Chi sq	67.6		Odds ratio:	3.01
P	0.000000		Log odds	1.10
	Pred. 0	Pred 1	% correct	
Observed 0	230	115	67	
Observed 1	138	208	60	
Forest losses 1973–2003				
Distance to road	−0.000069	0.000024	7.99423	0.004693
North	0.397571	0.108263	13.48546	0.000240
Distance to water	−0.000198	0.000081	5.98238	0.014449
Precipitation	0.001217	0.000177	47.45072	0.000000
Distance to shrubland	−0.002356	0.000900	6.86140	0.008808
Distance to grassland	−0.000877	0.000179	23.96758	0.000001
AIC	1173			
L. Radio Chi sq	65.6		Odds ratio:	2.45
P	0.000000		Log odds	0.90
	Pred. 0	Pred 1	% Correct	
Observed 0	248	181	58	
Observed 1	164	294	64	

Variables were selected by step-wise regression followed by AIC test of the best models

mainly explained by precipitation and distance to grasslands and water. During the last three decades forest losses became increasingly important, balancing its expansion (Fig. 3), being associated with northern aspects of higher rainfall areas close to shrublands, grasslands, rivers, lakes, and roads (Table 5).

Discussion

Dynamics of change in forest cover

Even though forest colonization on former shrublands in the region is considered a slow and diffuse process associated with availability of nursing plants

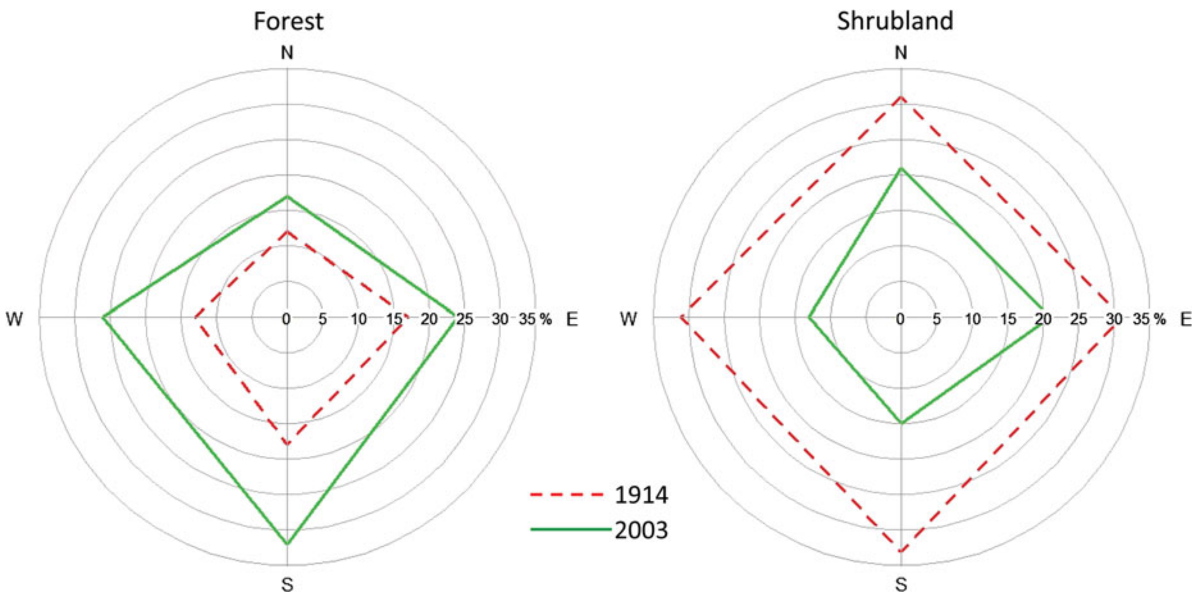


Fig. 4 Influence of aspect on the distribution of forest and schrubland. Forests were more common on South- and East-facing aspects at the beginning of the study period, showing the largest gains on West and South-facing aspects. Shrublands were evenly distributed at the beginning of the study period, being more persistent on North and East-facing aspects during the last 90 years

(Kitzberger et al. 2000), periods of higher precipitations (Villalba and Veblen 1997), reduction of grazing pressure from livestock (Raffaele et al. 2011), and masting years (Heinemann 2007; Sanguinetti and Kitzberger 2008), our results indicate that during the last century, Northern Patagonian forests expanded to almost 50% of historically burned land, and more than 60% of the shrublands of the study area. However, this trend was far from homogeneous in time and space: net forest expansion took place mainly during the period 1914–1973, probably favored by a wet climatic period (c. 1920s–1940s, Villalba and Veblen 1997), and has shown a marginal retraction since then (Fig. 3). Although, forest gains remained high during the last 30 years, substantial areas of forests were converted to grasslands and shrublands as a result of recent fires associated to extremely dry springs (Mermoz 2002). Forest expansion concentrated on southern and western aspects were local environmental conditions such as lower levels of direct insulation and higher precipitation may have facilitated seedling establishment (Fig. 4), whereas most recent forest fires originated on shrublands along north-facing aspects in the vicinity of roads and urban areas (Mermoz et al. 2005).

The main predictors of forest expansion (i.e., mean annual precipitation, high-elevation, and southerly or easterly aspects) relate to higher moisture availability. Mechanistically, higher moisture may create better (or more) opportunities for successful tree seedling germination and survival (Heinemann and Kitzberger 2006; Tercero-Bucardo et al. 2007), and conditions for less severe fires (higher tree survival), providing more seed sources and favorable microenvironments for tree establishment (Kitzberger et al. 2005). Distance to roads is also significantly related to forest expansion, indicating the negative impact of human-related activities on forest establishment, growth, and survival.

In order to trigger the forest expansion described above, seed sources have to be locally available because the dominant forest tree species disperse mainly in the vicinity of seed trees (Kitzberger 1994), showing no adaptations for long-distance dispersal. The hilly terrain of the study region, characterized by rocky outcrops, creeks, small streams, and a dense network of rivers and lakes may have resulted in a large number of small, unmapped refuges where individuals and small groups of fire-sensitive tree species survived the large fires of last century. We propose that a large number of small unburned forest patches triggered the extensive expansion documented here, and that the original map was too coarse for detecting these local seed sources.

Throughout last century, forest retraction was consistently associated with north-facing slopes and lower precipitation, indicating that forests are vulnerable to climatic-related dieback events or drought-induced severe fires. Drought-triggered mortality of some dominant tree species have been documented recently (Suárez et al. 2004; Suárez and Kitzberger 2008) and may become a novel path of forest retraction under predicted climatic scenarios for the coming century (Villalba et al. 2005). During the last three decades, loss of forests is associated with the vicinity of roads a pattern found in previous local studies (Mermoz 2002; Mermoz et al. 2005), indicating the importance of human-related fire ignitions on more recent forest losses. The negative relation between forest losses and distance to grasslands and shrublands may imply that interface fires that start in these communities are an important driver of forest retraction.

Shrubland retraction and fire dynamics

Shrublands showed a rather continuous rate of decrease during the last 100 years, but were more persistent on northern and eastern aspects (Fig. 4), where xeric conditions may reduce the likelihood of seedling establishment, and favor the spread of natural fires. Unlike the initial period, where most losses of shrublands were due to replacement by forests (Fig. 3), almost 70% of the shrublands lost during the last three decades have been replaced by grassland, a land cover class that is much more resistant to colonization by forests.

Human settlement in the region followed the main valleys: converting forests to grasslands for livestock raising. We propose that the large fires of last century may have triggered the development of a dichotomous landscape: fire-tolerant plant communities will persist under slightly more xeric conditions, close to roads and urban areas due to a combination of higher flammability, lower recruitment of forest trees, and high ignition frequency. On the other hand, fire-intolerant tree species will continue to expand under more mesic conditions and away from human-related disturbances due to a combination of a lower flammability of closed forests, favorable conditions for seedling establishment in remaining shrublands and infrequent ignitions.

Novel land uses and prospective land cover changes

The most expanding land uses in the region are pine plantations and urbanization. Both activities are mostly developing on former shrublands and grasslands being associated to roads, that may hinder forest expansion through reduced opportunities for establishment (Nuñez and Raffaele 2007), age-increasing flammability (Covington and Moore 1994), and higher ignition frequency (Mermoz 2002), reinforcing the pattern documented for the period 1973–2003. Whereas forest plantations of coniferous species are still marginal in the study region; they are the main cause of forest loss in northwestern Patagonia (Echeverría et al. 2006; Aguayo et al. 2009). Further, extensive plantations of fire-tolerant pine and eucalypt species are expanding as an economically attractive alternative land use for secondary forests in tropical and subtropical regions around the world.

Many boreal, temperate, sub-alpine, and tropical forests, and even some temperate shrublands, are driven by large stand-replacing fires associated with exceptional weather conditions (Johnson et al. 2001; Veblen et al. 2008; Brown 1998; Moritz et al. 2004). In these systems, fires of anthropogenic origin have proven to promote the development of dichotomous landscapes, where fire-adapted shade intolerant species dominate areas of recurrent disturbance and forests of low flammability persist in less accessible or pristine areas (Cochrane et al. 1999; Perry and Enright 2002; Odion et al. 2010). Replacement of secondary forests by large-scale plantations of species characterized by age-increasing flammability, rapid growth and fire-adapted reproduction may make the process of fragmentation of pristine forests more difficult to revert.

Land cover change dynamics and climatic variation

The process of forest expansion documented in this study may have been triggered by a period of higher precipitation (Villalba and Veblen 1997), whereas extremely dry weather has been proposed as the main cause of forest dieback (Suárez et al. 2004) and recent large fires (Mermoz 2002; Mermoz et al. 2005). Under a scenario of increasing climatic variability and high ignition frequency associated with human activity, the process of forest expansion documented in this study may be reverted within a few decades.

Unlike landscapes driven by age-increasing flammability, forests with low flammability of mature close-canopy stages may strongly benefit from reductions in fire ignitions (Kitzberger et al. in press). There is a growing awareness that historical land uses may lead to fire-maintained pyrophylic/pyrophobic dichotomous landscapes in many regions of the world (e.g., Perry and Enright 2002; Mermoz et al. 2005; Odion et al. 2010). Future research should explore the consequences of climatic variation, fire-fighting policy, and novel land uses on the dynamics of these systems.

Acknowledgments The authors thank the researchers of Laboratorio Ecotono and two anonymous referees for valuable discussions and comments on this manuscript. This study was funded by ANPCyT, PICTO Forestal 16-36801, and ReForLan (FP6-INCO # 32132). J.H.G, T.K., and A.C.P. are researchers of CONICET.

References

Aguayo M, Pauchard A, Azócar G, Parra O (2009) Cambio del uso del suelo en el centro sur de chile a fines del siglo. Entendiendo la dinámica espacial y temporal del paisaje. Rev Chil Historia Nat 82:361–374

Brown N (1998) Out of control: fires and forestry in Indonesia. Trends Ecol Evol 13:41–44

Bruno J, Martín G (1982) Los incendios forestales en los parques nacionales. Report Administración de Parques Nacionales, Buenos Aires

Cochrane MA, Alencar A, Schulze MD, Souze CM, Nepsatd DC, Lefebvre CP, Davidson EA (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284:1832–1835

Covington WW, Moore MM (1994) Southwestern ponderosa forest structure: changes since Euro-American settlement. J For 92:39–47

Echeverría C, Coomes D, Salas J, Rey-Benayas JM, Lara A, Newton A (2006) Rapid deforestation and fragmentation of Chilean temperate forests. Biol Conserv 130:481–494

Eriksen W (1971) Betriebsformen und probleme der viehwirtschaft am rande der Argentinischen Südkordillere. Z Ausl Landwirtsch 10:24–27

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. BioScience 53:77–88

Graham SA, Harrison RP Jr, Westell CE Jr (1963) Aspens: phoenix trees of the great lakes region. University Michigan Press, Ann Arbor

Grau HR, Aide TM, Zimmerman JK, Thomlinson JR, Helmer E, Zou X (2003) The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. Bioscience 53:1159–1168

Grau HR, Hernández ME, Gutierrez J, Gasparri NI, Casavecchia MC, Flores EE, Paolini L (2008) A peri-urban neotropical forest transition and its consequences for environmental services. Ecol Soc 13(1):35

Hall B, Motzkin G, Foster DR, Syfert M, Burk J (2002) Three hundred years of forest and land-use change in Massachusetts, USA. J Biogeogr 29:1319–1335

Heinemann K (2007). Aspectos espaciales y temporales del establecimiento de Nothofagus pumilio en claros de bosques maduros en los extremos de un gradiente ambiental en el Noroeste de la Patagonia. Ph.D. Thesis, Universidad Nacional del Comauhe

Heinemann K, Kitzberger T (2006) Effects of position, understory and coarse woody debris on tree regeneration in two environmentally contrasting forests of northwestern Patagonia: a manipulative approach. J Biogeogr 33:1357–1367

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Idrissi Andes (2006) http://www.clarklabs.org

INDEC 2001. Censo Nacional de Poblacion, Hogares y Viviendas 2001. http://www.indec.gov.ar/webcenso/publicaciones/publicaciones.asp

Johnson EA, Miyanishi K, Bridge RJ (2001) Wildfire regime in boreal forest and the idea of suppression and fuel buildup. Conserv Biol 15:1554–1557

Kitzberger T (1994) Fire regime variation along a northern Patagonian forest-steppe gradient: stand and landscape response. Ph.D. Thesis, Department of Geography, University of Colorado, Boulder

Kitzberger T, Aráoz E, Gowda JH, Mermoz M, Morales JM Decreases in fire spread probability with age promotes alternative states, reduced resilience to climate variability and large fire regime shifts. Ecosystems (in press)

Kitzberger T, Veblen TT (1997) Influences of humans and ENSO on fire history of *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina. Ecoscience 4:508–520

Kitzberger T, Veblen TT (1999) Fire-induced changes in northern Patagonian landscapes. Landsc Ecol 14:1–15

Kitzberger T, Veblen TT, Villalba R (1997) Climatic influences on fire regimes along a rainforest-to-xeric woodland gradient in northern Patagonia, Argentina. J Biogeogr 23: 35–47

Kitzberger T, Steinaker DF, Veblen TT (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology 81:1914–1924

Kitzberger T, Raffaele E, Heinemann K, Mazzarino MJ (2005) Effects of fire severity in a north Patagonian subalpine forest. J Veg Sci 16:5–12

Mermoz (2002) Detección y mapeo de incendios forestales en los Parques Nacionales del Nor-Patagonia, período 1985–1999. Administración de Parques Nacionales. http://www.conae.gov.ar/WEB_Emergencias/Links_de_la_Izquierda/Incendios/Informes_Realizados/Deteccion_Mapeo_Nor_Patagonia_85-99/Deteccion_Mapeo_Nor_Patagonia_85-99.htm (Unpublished Report)

Mermoz M, Kitzberger T, Veblen TT (2005) Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology 86:2705–2715

Moritz MA, Keeley JA, Johnson EA, Schaffner AA (2004) Testing a basic assumption of shrubland fire management: How important is fuel age? Frontiers Ecol Environ 2:67–72

Nuñez MA, Raffaele E (2007) Afforestation causes changes in post-fire regeneration of native shrubland communities of northwestern Patagonia, Argentina. J Veg Sci 18:827–834

Odion DC, Moritz MA, DellaSala DA (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. J Ecol 98:96–105

Perry GLW, Enright NJ (2002) Humans, fire and landscape pattern: understanding a maquis-forest complex, Mont Do, New Caledonia, using a spatial 'state-and-transition' model. J Biogeogr 29:1143–1158

Petit CC, Lambin EF (2002) Impact of data integration technique on historical land-use/land-cover change: comparing historical maps with remote sensing data in the Belgian Ardennes. Landsc Ecol 17:117–132

Raffaele E, Veblen TT, Blackhall M, Tercero-Bucardo N (2011) Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. J Veg Sci 22:59–71

Rhemtulla JM, Mladenoff DJ, Murray KC (2007) Regional land-cover conversion in the U.S. upper Midwest: magnitude of change and limited recovery (1850–1935–1993). Landsc Ecol 22:57–75

Sanguinetti J, Kitzberger T (2008) Patterns and mechanisms of masting in the large-seeded southern hemisphere conifer *Araucaria araucana*. Austral Ecol 33:78–87

Schlichter T, Laclau P (1998) Ecotono estepa-bosque y plantaciones en la Patagonia norte. Ecol Austral 8:285–296

Schulte LA, Mladenoff DJ, Crow TR, Merrick LC, Cleland DT (2007) Homogenization of U.S. Great Lakes forests due to land use. Landscape Ecol 22:1089–1103

Suárez ML, Kitzberger T (2008) Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. Can J For Res 38:3002–3010

Suárez ML, Kitzberger T (2010) Differential effects of climate variability on forest dynamics along a precipitation gradient in northern Patagonia. J Ecol 98:1023–1034

Suárez ML, Ghermandi L, Kitzberger T (2004) Factors predisposing episodic drought-induced tree mortality in *Nothofagus*: site, climatic sensitivity and growth trends. J Ecol 92:954–966

Tercero-Bucardo N, Kitzberger T, Veblen TT, Raffaele E (2007) A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. J Ecol 95:771–779

Veblen TT, Lorenz DC (1987) Post-fire stand development of *Austrocedrus–Nothofagus* forests in Patagonia. Vegetatio 73:113–126

Veblen TT, Lorenz DC (1988) Recent vegetation changes along the forest/steppe ecotone in northern Patagonia. Ann Assoc Am Geogr 78:93–111

Veblen TT, Kitzberger T, Lara A (1992a) Disturbance and vegetation dynamics along a transect from rain forest to Patagonian shrublands. J Veg Sci 3:507–520

Veblen TT, Mermoz M, Martin C, Kitzberger T (1992b) Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conserv Biol 6:71–83

Veblen TT, Kitzberger T, Villalba R, Donnegan J (1999) Fire history in northern Patagonia: the roles of humans and climatic variation. Ecol Monogr 69:47–67

Veblen TT, Kitzberger T, Raffaele E, Mermoz M, González ME, Sibold SJ, Holz A (2008) The historical range of variability of fires in the Andean-Patagonian *Nothofagus* forest region. Int J Wildland Fire 17:724–741

Villalba R, Veblen TT (1997) Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. J Ecol 85:113–124

Villalba R, Masiokas M, Kitzberger T, Boninsegna JA (2005) Biogeographical consequences of recent climate changes in the southern Andes of Argentina. In: Huber UM, Bugmann HKM, Reasoner MA (eds) Global change and mountain regions. Advances in global change research, vol 23, Springer-Verlag, p 650, ISBN: 1-4020-3506-3

Willis B (1914) El Norte de la Patagonia. Dirección de Parques Nacionales, Buenos Aires